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An Ecological Study of Helminths of Some Wyoming Voles (*Microtus* spp.) with a Description of a New Species of *Nematospiroides* (Heligmosomidae: Nematoda).[1]

MERLE L. KUNS & ROBERT RAUSCH.[2]

(Text-figures 1-7).

PROBLEM.

Studies on parasitic infections may be made with special reference to either a parasite or a host group. Taxonomic studies are usually concerned with a group of closely related parasites which may have been collected from a wide variety of hosts. This is the most common method of obtaining data, and is one essential step for the proper understanding of parasite taxonomy. However, another method which involves consideration of the problems of parasitism within a group of closely related hosts, facilitates the understanding of such ecological problems as distribution and control and emphasizes evolutionary and zoogeographic implications. It is this latter approach to the problem of host-parasite relationships in which we have been primarily interested.

It is the purpose of this paper to present data resulting from an ecological study of the helminth parasites of voles of the genus *Microtus* collected during the summer of 1948 from various habitats in the Jackson Hole region of Wyoming.

The ecological aspects of parasitism in mouse-like rodents have until recently received little attention. Elton *et al* (1931) studied the helminths of *Apodemus sylvaticus* L. and reported a correlation of parasitism and age. Rodent parasites were studied in North Carolina by Harkema (1936), with some reference to seasonal fluctuation. An intensive study on the ecology of certain mouse-like rodents in the Transcaucasus region of Russia was carried on by Kirschenblatt (1938). Kirschenblatt's work has been discussed in a previous paper (Rausch & Tiner, 1949). Rankin (1945) studied the helminth parasites of various rodents in the state of Washington. At the present time, the most complete study of the ecology of helminths parasitic in voles is that of Rausch & Tiner (1949), in which several species of parasites are considered.

OBSERVATIONS AND RESULTS.

Eleven species of parasitic helminths were recovered from 103 representatives of four species of *Microtus* (Cricetidae) collected in the Jackson Hole region of Wyoming. The species of voles considered were *M. pennsylvanicus modestus* (Baird), *M. montanus nanus* (Merriam), *M. longicaudus mordax* (Merriam) and *M. richardsoni macropus* (Merriam). The techniques used in connection with the collection of the parasites was the same as that outlined in previous publications (Rausch & Tiner, 1948; 1949).

Mammal population data were obtained according to the method of Bole (1939). This method consists of saturating representative quadrats of one-half acre (22,500 square feet) with snap traps for a three-day period. This allows for a relative idea of rodent population density per unit area.

The following helminths were collected: *Quinqueserialis hassalli* (McIntosh & McIntosh, 1934); *Andrya primordialis* (Douthitt, 1915); *A. macrocephala* (Douthitt, 1915); *Paranoplocephala infrequens* (Douthitt, 1915); *P. variabilis* (Douthitt, 1915); *P. borealis* (Douthitt, 1915); *Hymenolepis horrida* (von Linstow, 1900); *Heligmosomum costellatum* (Dujardin, 1845); *Nematospiroides microti* n. sp.; *Syphacia obvelata* (Rudolphi, 1802); and *Trichuris opaca* Barker & Noyes, 1915. Of these, all are known to be common parasites of North American voles except *H. horrida, H. costellatum* and *N. microti.*

Hymenolepis horrida (Text-figs. 1 & 2) and *Heligmosomum costellatum* (Text-figs. 3 & 4) are here recorded for the first time from North America, although they are known from various species of Eurasian voles. One of us (R. R.) has recovered these species from microtine rodents in Alaska, *H. horrida* occurring commonly in *Dicrostonyx, Lemmus, Microtus* and *Clethrionomys*, and *H. costellatum* in *Microtus*. It is suggested that these species are essentially

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[2] Department of Biological Sciences, Purdue University, and U. S. Public Health Service, Anchorage, Alaska.

arctic and subarctic in distribution in North America with southward extensions in the alpine zone of the Rocky Mountains.

The available descriptions of *Heligmosomum costellatum* are at variance, especially with regard to the interpretation of cuticular structures (Travassos & Darriba, 1929; Desportes, 1943). In view of the position which *H. costellatum* occupies as type of the genus on which the family Heligmosomidae Cram, 1927, is based, it seems desirable to supplement existing descriptions with the following observations based on abundant material from Wyoming voles. All measurements are in millimeters unless otherwise specified.

Heligmosomum costellatum (Dujardin, 1845). (Text-figs. 3 & 4).

Slender, rather small nematodes, with the characters of the genus; red in life, not spirally coiled. Cuticle with well-developed oblique longitudinal lines or ridges originating in the left lateral field and progressing obliquely posteriad to end in the right lateral field. Esophagus long, clavate and terminating in a short, slightly modified portion.

Male: body length 7.0-10.6, maximum width 0.125-0.152. Cephalic cuticular dilatation 0.069-0.10 long by 0.080-0.095 in diameter. Nerve ring 0.185-0.210, excretory pore 0.354-0.52 from the anterior extremity. Esophagus 0.4-0.5 long by 0.053-0.058 in maximum width. Cervical papillae apparently absent. Reproductive organs simple; testis originating 1.3-3.6 from the anterior extremity and narrowing to form a short vas deferens near the midpoint of the body. Seminal vesicle a slightly expanded portion of the genital tract narrowing gradually to form the ejaculatory duct. Pre-bursal papillae slender and very difficult to observe. Bursa large and slightly asymmetrical, the right lateral lobe being somewhat larger than the left. Ventral rays widely divergent, with a common stem; latero-ventral large and muscular. Lateral rays slender and with a common stem; the postero-lateral widely divergent from the group. Externo-dorsal rays long and slender, isolated at the point of origin. Dorsal ray originating near the bases of the externo-dorsals; small and difficult to observe, 0.050-0.056 long and branched to form two short, curved lateral rami and two longer, straight median rami. Dorsal lobe much reduced and difficult to observe. Genital cone with two slender papillae which encircle the protruded spicules. Spicules similar, slender, 0.01-0.013 in diameter at the proximal end, 0.85-0.99 long; each bifurcate 0.08-0.10 from the base to form two sub-equal processes, the longer ending in a diminutive hook. Gubernaculum apparently absent.

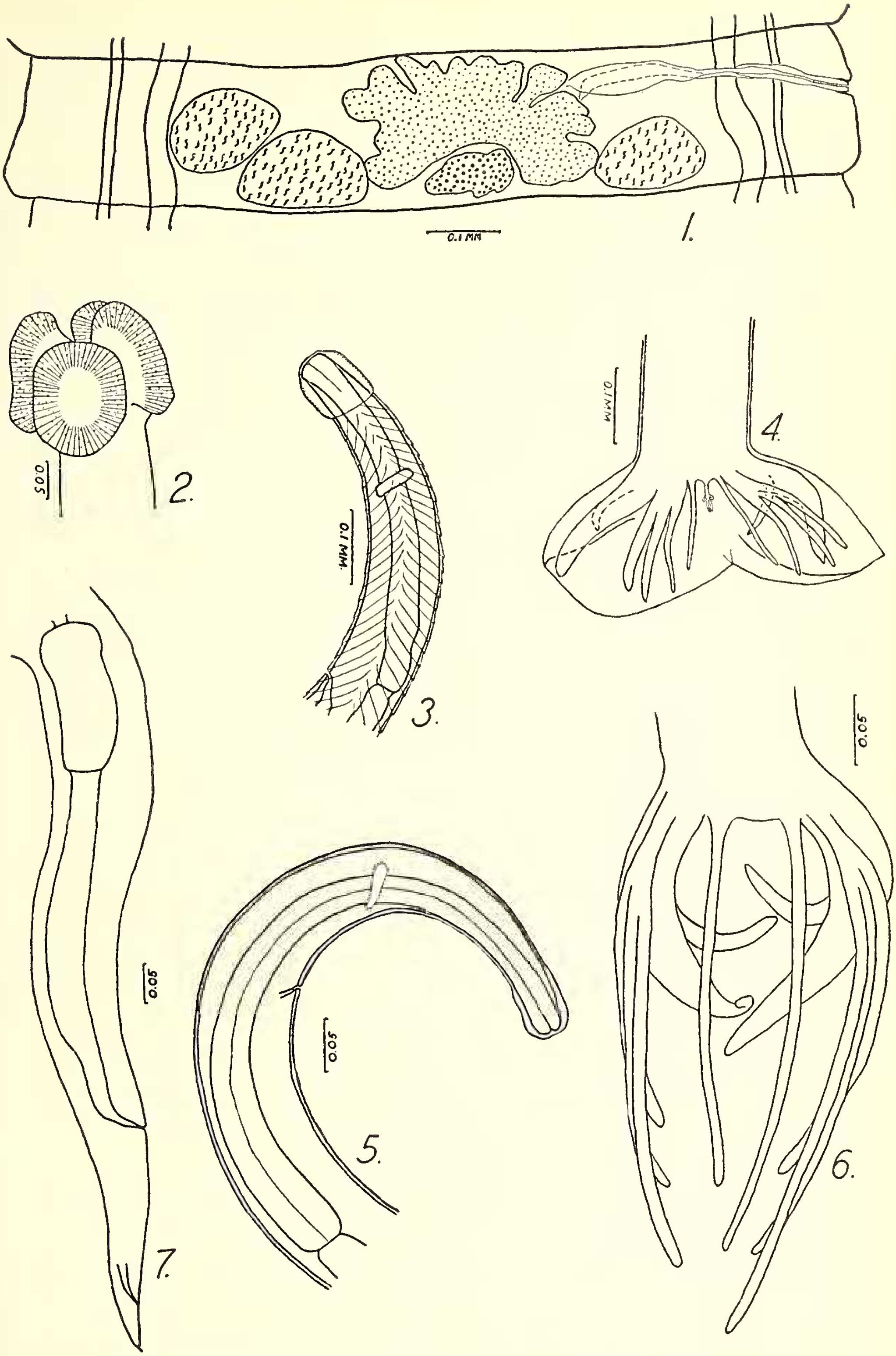
Female: body 8.5-15.0 long by 0.135-0.18 in maximum width. Cephalic cuticular dilatation 0.085-0.125 long by 0.083-0.098 in diameter. Nerve ring 0.175-0.225; excretory pore 0.35-0.51 from the anterior extremity. Esophagus 0.48-0.51 long by 0.055-0.06 in maximum width. Reproductive organs simple; ovary originating 3.5-5.0 from the anterior extremity, looping forward occasionally as it progresses posteriorly to form a short, indistinct oviduct joining the uterus about one-fourth the length from the posterior end. Ovejector well-developed; consisting of anterior, thick-walled infundibulum 0.16-0.21 in length, a sphincter and a posterior muscular ejectrix, lined with cuticle and 0.125-0.20 long; both sphincter and ejectrix with a prominent external layer of obliquely arranged muscle fibers. Vagina long, lined with cuticle and with an S-shaped portion near the midpoint. Vulva large, conspicuous, and located 0.32-0.48 from the posterior extremity. Tail 0.064-0.077 long, attenuated and terminated by a cuticular spine 0.012-0.015 in length. Eggs thin-shelled; 0.099-0.117 long by 0.049-0.053 wide. Embryos in the morula stage at the time of deposition.

Several nematodes recovered from voles in only the alpine zone of the Jackson Hole region appear to represent an undescribed species of *Nematospiroides* for which the name *N. microti* is proposed.

Nematospiroides microti n. sp. (Text-figs. 5-7).

Specific diagnosis: Small, spirally-coiled nematodes with the characters of the genus. Cuticle with minute transverse striations and 16 conspicuous longitudinal lines or ridges. Cephalic cuticular dilatation slightly asymmetrical. Cervical papillae not observed. Esophagus claviform. Reproductive organs simple.

Male: 5.8-6.0 long by 0.08-0.10 in maximum width. Cephalic cuticular dilatation measuring 0.052-0.065 in length by 0.038 in diameter. Diameter of head 0.027-0.028. Nerve ring 0.16-0.19 and excretory pore 0.30-0.34 from the anterior extremity. Esophagus 0.59-0.60 long, increasing in width from 0.024 anteriorly to a maximum of 0.045-0.053 near its junction with the intestine. Pre-bursal papillae apparently absent. Testis simple, originating about 0.15 posterior to the intestino-esophageal junction. Seminal vesicle short, narrowing to form ejaculatory duct about 2.25 from the posterior extremity. Bursa measuring 0.40-0.45 by 0.15-0.18 wide in the closed or folded position usually observed, asymmetrical, the right lateral lobe being larger than the left. Ventral rays widely divergent and with a common stem. Ventro-ventral small, slender, curving toward the mid-line to end 0.15-0.16 from the cloacal orifice. Lateral rays slender, elongate, parallel for most of their length, with a common stem and graduated in length; medio-lateral and postero-lateral rays divergent near the tips, the postero-lateral nearly attaining the bursal margin. Externo-dorsal rays slender, elongate and widely separated at the base. Dorsal ray 0.06-0.065 long, arising separately, and directed abruptly ventrad



TEXT-FIGS. 1-7. **1.** *Hymenolepis horrida*, mature proglottid. **2.** *Hymenolepis horrida*, scolex. **3.** *Heligmosomum costellatum*, anterior end. **4.** *Heligmosomum costellatum*, bursa copulatrix. **5.** *Nematospiroides microti* n. sp., anterior end. **6.** *Nematospiroides microti* n. sp., bursa copulatrix. **7.** *Nematospiroides microti* n. sp., posterior end of female.

toward the cloacal orifice where it branches to end in four slender points. Spicules simple, equal, filiform, 0.01 wide at the base and 2.08-2.20 in length; retracted portion enclosed in a well-developed, non-protrusible sheath. Gubernaculum apparently absent.

Female: 8.0-10.5 in length by 0.12-0.13 in maximum width. Cephalic cuticular dilatation 0.062-0.080 long by 0.046-0.048 in diameter. Diameter of head 0.032-0.035. Nerve ring located 0.20 and excretory pore 0.31 from anterior extremity. Esophagus 0.68-0.69 long by 0.05-0.062 in maximum width near the posterior end. Ovary originating 1.4-2.0 from the anterior end. Oviduct indistinct. Ovejector well developed, consisting of an anterior thick-walled infundibulum 0.16-0.19 long and a median sphincter which is fused with the muscular ejectrix to form an organ 0.17-0.18 in length. Vagina and ejectrix with a cuticular lining. Vulva located 0.28-0.32 from the posterior extremity. Tail 0.058-0.064 in length, attenuated, and terminating in a minute spine 0.01-0.012 in length. Eggs thin-shelled, 0.078-0.082 long by 0.04-0.043 in width. Embryo in early cleavage at the time of deposition.

Hosts: *Microtus montanus nanus* (type host) and *Microtus richardsoni macropus.*

Habitat: Small intestine.

Type locality: Brooks Mountain, Fremont County, Wyoming.

Holotype: Mature male, U. S. National Museum Helminthological Collection No. 46394.

Paratype: Mature female, U. S. National Museum Helminthological Collection No. 46394.

This species is readily distinguished from other members of the genus by the elongate lateral and externo-dorsal rays of the male.

The Jackson Hole region of Wyoming includes the valley of the Snake River from Yellowstone National Park on the north to the Hoback River on the south, and from the continental divide west to the Grand Teton Range. The valley slopes from about 7,000 feet above sea level in the north to 6,000 feet in the south, and has an area of about 337 square miles. Voles of the genus *Microtus* were found in six rather well defined habitats within this general area. The habitats are discussed separately.

Habitat I: Sage flats. Altitude 6,500 feet. Host population density about 1.0 vole per acre. A considerable portion of the valley floor between the towns of Moran and Jackson is covered by a moderately dense growth of sagebrush (*Artemesia* spp; mainly *A. tridentata* Nutt.). According to the classification of Merriam, this is the only habitat in the Jackson Hole region characteristic of the transition life zone. One of the quadrats located in this habitat (5 miles south of Moran) yielded only two specimens of *Microtus montanus nanus,* both of which were negative for helminth parasites. Although this represented an inadequate sample, it is believed that the degree of parasitism in this habitat must be very low.

Habitat II: Aspen consocies. Altitude 6,700 feet. Host population density about 3.5 voles per acre. This vegetation type (*Populus tremuloides* Michx.) occurs in several small, relatively dry areas within the Wildlife Park and forms a part of the broad ecotone between the lower limits of the Canadian and the upper limits of the transition life zone. *Microtus longicaudus mordax* was collected only in this habitat. Two of five individuals were parasitized, one with a single specimen of *Paranoplocephala infrequens* and another with two of *Syphacia obvelata.* One of three specimens of *M. montanus nanus* taken from this habitat harbored 23 *S. obvelata* in the cecum.

Habitat III: Dry meadow. Altitude 6,700 to 7,000 feet. Host population density moderate (estimated at 10 per acre). Several areas in the vicinity of the Wildlife Park supported a rather dense growth of medium-height grasses and herbaceous plants. This habitat is classified in the transition-Canadian ecotone. Because of the drainage or topography, this habitat is too dry to support the sedges and willows of adjacent lowland areas. Collections were made near Two-ocean Lake, Emma Matilda Lake, and Elk Ranch. Twenty-two specimens of *Microtus montanus nanus* from this habitat were parasitized by the following helminths: *Andrya primordialis* (18 per cent.); *Paranoplocephala infrequens* (18 per cent.); *P. borealis* (5 per cent.); *P. variabilis* (5 per cent.); *Syphacia obvelata* (9 per cent.). Fourteen (64 per cent.) of these animals were negative for helminths.

Habitat IV: Willows and wet meadows. Altitude 6,700 feet. Host population density moderate (about 15 per acre). Wet or swampy areas in the transition-Canadian ecotone were common in the vicinity of streams in the Park, and are characterized by a dense growth of willows (*Salix* spp.) interspersed with open meadows of grasses and sedges. *Microtus pennsylvanicus modestus* was found only in this habitat, as was the trematode *Quinqueserialis hassalli.* The latter is presumably limited by the distribution of the snail intermediate host. The incidence of infection of voles in this habitat is summarized in Table I.

Habitat V: Sub-alpine meadow. Altitude 9,200 feet. Host population density high (estimated at 40 per acre). Two species of *Microtus* (*M. richardsoni macropus* and *M. montanus nanus*) were collected in the moist, park-like openings along small streams in the spruce-fir (*Picea parryana-Abies* sp.) climax forest of the Canadian life zone. Two areas near Togwotee Pass, Fremont County, Wyoming, were selected for study, and ten specimens of *M. richardsoni macropus* collected there were parasitized by helminths as follows: *Andrya primordialis* (30 per cent.); *A. macrocephala* (10 per cent.); *Trichuris opaca* (20 per cent.). Two voles were not infected by helminths. *Microtus montanus* also occurred in this habitat, but no examinations were made of this species.

Habitat VI: Alpine meadow. Altitude 11,000 feet. Host population density about 61 voles per acre. Large areas of flat or gently sloping meadow covered the tops of some of the mountains at the eastern margin of the region under consideration. These meadows were usually 1,000 feet or more above timberline and were covered with deep snow during most of the year. The vegetative cover was low but very dense. The alpine buttercup (*Ranunculus* sp.) and a species of *Mertensia* were characteristic of this habitat. The top of Brooks Mountain, Fremont County, Wyoming, was selected for study because of its accessibility. Eighty-one per cent. of 21 *Microtus montanus nanus* and 60 per cent. of 10 *M. richardsoni macropus* collected in this habitat were infected with the helminths listed in Table II. Two cestodes and one nematode from these hosts were damaged and specific determination was not possible. These are listed in Table II as *Andrya* sp., *Paranoplocephala* sp. and *Nematospiroides* sp.

Discussion.

The habitats included in this study were unusually varied, ranging from the hot, dry sage flats to areas of swamp or perennial snow. Since they were concentrated in an area less than 35 miles in diameter, an excellent opportunity was afforded for an ecological investigation in relation to helminth parasites.

One species of vole (*Microtus montanus nanus*) was found to range throughout the region and was absent only from the coniferous forests where the small, succulent forms of vegetation, apparently required as a food supply, were lacking. The three other species of voles collected during the course of this study apparently were much more demanding in their habitat requirements. *Microtus pennsylvanicus modestus* was observed to be restricted to swampy areas supporting dense growths of sedges and willows (Habitat IV). *Microtus longicaudus mordax* was found only in the open groves of aspen (Habitat II). The large water-vole, *Microtus richardsoni macropus*, was apparently restricted to the subalpine meadows occurring along streams in the spruce-fir forests at high altitudes (Habitat V) and to the alpine meadows occurring above timber-line (Habitat VI).

This unique pattern in the distribution of four species of the same genus of voles offered an opportunity for the evaluation of host specificity as opposed to ecological factors in regard to the geographic distribution of certain parasites. The parasites encountered in any one habitat showed neither preference for *M. montanus nanus*, the only vole occurring in all habitats studied, nor for any other species of vole limited to a single specific habitat (see Tables I and II). The examination of Table III shows that some helminths were generally distributed, while others were restricted in their distribution. Since host specificity does not explain this pattern of parasite distribution, other factors must be considered.

Host population density may influence the distribution and incidence of infection by these helminths. Although the greatest numbers of parasites, both qualitative and quantitative, occurred in habitats where host density was greatest, it seems unlikely that host density is the only factor involved.

The distribution patterns of some of the parasites encountered appear to be more understandable when their life cycles are taken into consideration. Although the intermediate host of *Quinqueserialis hassalli* has not been determined, it is presumably a gastropod mollusc. Herber (1942) reported a snail, *Gyraulus parvus* (Say), as the intermediate host of *Q. quinqueserialis* (Barker & Laughlin, 1911), a species closely related to the one with which we are concerned. This species develops through a sporocyst and two redial generations in the snail, and the

TABLE I.

Incidence of Parasitism for Voles Collected in Habitat IV (Wet Meadows).

	Microtus pennsylvanicus modestus	*Microtus montanus nanus*	Total for Habitat IV
Number of hosts examined	15	14	29
Quinqueserialis hassalli	20%	7%	14%
Andrya primordialis	13%	14%	14%
Andrya macrocephala	13%	21%	17%
Paranoplocephala infrequens	33%	29%	31%
Syphacia obvelata	20%	14%	17%
% of hosts infected with one or more of the above species	60	64	62

emerging cercariae encyst on aquatic vegetation. Assuming a similar life cycle for *Q. hassalli*, only those voles which include a suitable habitat for the intermediate host within their home range would be exposed to infection. The apparent limitation of *Q. hassalli* to one habitat would support this.

If it can be assumed that mites serve as the intermediate host for the anoplocephaline cestodes encountered, the distribution of mites would determine the occurrence of such cestodes. This has been more completely discussed in a previous paper (Rausch & Tiner, 1949).

All nematodes collected in connection with the present study are assumed to have direct life cycles. If this is true, the distribution and abundance of susceptible hosts, coupled with conditions favorable to the survival of infective eggs and larvae, would strongly influence the occurrence of such parasites. The life cycle of *Hymenolepis horrida* is unknown.

Four species, viz., *Hymenolepis horrida*, *Heligmosomum costellatum*, *Nematospiroides microti* and *Trichuris opaca*, were restricted to highland habitats (V and VI). Since both of these habitats are near or above timber line (9,200 to 11,000 feet) they are characterized by prolonged winter conditions of deep snow, low temperature and high winds. Extensive snow drifts were observed in the alpine habitat during the first week of July. The densest populations of both hosts and parasites were encountered in these habitats. The permanent dampness and coolness here would perhaps account for better survival of nematode eggs and larvae, and also contribute to a luxuriant growth of vegetation upon which the voles are dependent for food. Previous work (Rausch & Tiner, 1949) would indicate that moisture is of great importance in connection with degree of abundance of vole parasites. This is true from both a qualitative and quantitative standpoint.

A suitable explanation for the restriction of four species of parasites to highland habitats appears to be lacking. It is noteworthy that *Hymenolepis horrida* and *Heligmosomum costellatum* are European parasites, not previously recorded from North America. Their occurrence only in the highland habitats in the Jackson Hole region and near sea level in Alaska may be of zoogeographic significance, but further study is necessary to allow any definite conclusions.

Summary.

An ecological and taxonomic study of the helminth parasites of voles (*Microtus* spp.) in the Jackson Hole region of Wyoming is reported.

Nematospiroides microti n. sp. from *Microtus montanus nanus* and *M. richardsoni macropus* is described and figured

A cestode, *Paranoplocephala infrequens*, and a nematode, *Syphacia obvelata*, were generally distributed throughout the region in all habitats except the sage flats.

A trematode, *Quinqueserialis hassalli*, was recovered only from voles collected near streams at low altitudes. This was presumably due to the localized distribution of the molluscan intermediate host.

Four helminths, viz., *Hymenolepis horrida*, *Heligmosomum costellatum*, *Nematospiroides microti* and *Trichuris opaca*, were restricted in their distribution to the alpine and sub-alpine meadows. Of these parasites, *H. horrida* and *H. costellatum* are reported for the first time from North America. Most of the other host and locality records are new.

TABLE II.

Incidence of Parasitism for Voles Collected in Habitat VI (Alpine Meadow).

	Microtus montanus nanus	*Microtus richardsoni macropus*	Total for Habitat VI
Number of hosts examined	21	10	31
Andrya primordialis	29%	20%	26%
Andrya macrocephala	5%	20%	10%
Andrya sp.	0	10%	3%
Paranoplocephala infrequens	29%	20%	26%
Hymenolepis horrida	10%	20%	13%
Heligmosomum costellatum	24%	40%	29%
Nematospiroides microti n. sp.	10%	10%	10%
Nematospiroides sp.	0	10%	3%
Syphacia obvelata	48%	30%	42%
% of hosts infected with one or more of the above species	81	60	74

TABLE III.

Helminth Parasites of Voles from Various Habitats in the Jackson Hole Region of Wyoming.

	Sage Flats	Aspen Groves	Dry Meadow	Willows & Wet Meadows	Sub-alpine Meadow	Alpine Meadow	Total for Region
Altitude in feet	6,500	6,700	6,700	6,700	9,200	11,000	—
Vole Population / acre	1	7	10*	15	40*	61	—
No. of vole species present	1	2	1	2	2	2	4
No. of voles examined	2	5	22	29	10	31	103
Syphacia obvelata	0	14%	9%	17%	30%	42%	24%
Paranoplocephala infrequens	0	14%	18%	31%	30%	26%	25%
Andrya primordialis	0	0	18%	14%	30%	26%	19%
Andrya macrocephala	0	0	0	17%	10%	10%	9%
Hymenolepis horrida	0	0	0	0	30%	13%	7%
Heligmosomum costellatum	0	0	0	0	10%	29%	10%
Paranoplocephala variabilis	0	0	5%	0	0	0	2%
Paranoplocephala borealis	0	0	5%	0	0	0	2%
Quinqueserialis hassalli	0	0	0	14%	0	0	4%
Trichuris opaca	0	0	0	0	20%	0	2%
Nematospiroides microti	0	0	0	0	0	10%	3%
% of hosts infected with one or more of the above species	0	28	36	62	80	74	60

* Estimated.

Available data indicate that host specificity was not a factor in restricting the distribution of parasites.

Although the greatest numbers of parasites, both qualitative and quantitative, occurred in habitats where host density was greatest, it seems unlikely that host density is the only factor involved.

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